Causes and Significance of Morphological Variation in Fishes

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Introduction

Many ichthyologists have tended to assume extreme positions as to whether observed differences between populations of a given species of fish are caused by genetic differences or merely by dissimilarities of environments. Early workers were inclined to regard differences, especially countable ones, as indicative of genetic divergence alone. Many of these forms were formally recognized as subspecies, or species (examples are cited in Jensen, 1944). The weight of thought swung the opposite direction after the discovery that characters could be altered through manipulation of the environment. Now ichthyologists commonly assume differences between populations of a species are environmentally induced unless a genetic basis can be demonstrated experimentally. The bulk of recent literature, however, is concerned primarily with the elucidation of the effect of environment on a given genetic stock. The problem of genetic divergence between populations of a fish species, or within a single population, has not received as much attention and evidence along these lines, therefore, is meager (but see Gordon, 1957).

It is essential to the progress of systematic ichthyology, as well as to the planning of experiments on this problem, that the nature of morphological variation in fishes be properly understood. Since the early papers by Hubbs, only Tåning (1952) has reviewed this subject. Tåning stressed the role of the environment in determining meristic characters, and also fostered the misleading notion of day-degrees.

The primary objective of the article at hand is to put forth arguments to support what is meant to be a more balanced point of view. Morphological clines, especially for those forms which have somewhat disjunct populations, are regarded as the consequences of environmental modifications coupled with adaptive genetic changes. In the course of writing the article it also became necessary to reconsider the problem of the production of variation in fishes, particularly, meristic variation. As a result, a refinement of Hubbs’s (1926) hypothesis has been developed to account for the genesis of meristic variation in the hope it may give direction to the design of future experiments.

Variation in Size and Shape

Variation in size and shape of fishes will not be treated as fully as meristic variation. More is known about meristic variation, so it is profitable to treat that subject in greater detail. Nonetheless, a synopsis of what is known about genetic and environmental factors in the control of size and shape of fishes should assist the reader in evaluating the major thesis of this article.

Differences in size and shape are apparent in comparisons between fish from waters of different temperatures. Almost invariably the more northern representatives of a species, or of a genus, are larger than those to the south (Hubbs, 1926; 1

1 The term meristic variation is used here in the widest sense, referring to all countable characters, though most of the discussion centers on variation in the number of fin rays and vertebrae.
Vladykov, 1934). The changes in body proportions have not been as thoroughly investigated as those in segmental structures, but some tentative generalizations can be made. Northern, slowly growing races of a species usually have smaller heads, eyes, maxillaries, and fins than do their southern counterparts, although opposite effects are not uncommon (Hubbs, 1926; Vladykov, 1934; Martin, 1949; and included references).

Growth rate apparently determines body shape by altering the timing of transition from one growth stanza to another (Huxley, 1932; Martin, 1949). Each growth stanza is recognized by a characteristic relative growth of the body part. The transition from one stanza to the next is usually abrupt and produces a new relationship between the growth of the part and the body as a whole. If the logarithms of the part, and of the length of the fish are plotted, a straight line is obtained for a given stanza. The transition to the next stanza is revealed by an inflection of the slope of the line. Differences in the relative sizes of body parts between fish of the same species are the results of changes in the timing of the inflections, not of the slopes of the lines. Because of this, growth changes in early life are particularly efficacious in modifying the form of the fish (Martin, 1949). Changes in relative growth sometimes occur at sexual maturity, but seldom after.

Evidently, the environment can modify the shape of a fish (Vladykov, 1934; Svärdson, 1953, and earlier references therein; Williams, 1954) by acceleration or retardation of the rate of development (Hubbs, 1926; Martin, 1949). But the scope and direction of such variation that is due to genetic differences is not understood, and research is sorely needed here. Martin (1949) noted that within a group of rainbow trout, Salmo gairdneri, the fish with small heads were the ones that grew slowly. Presumably genetic differences were responsible for the divergence. However, the rainbow trout reared at high temperatures, consequently faster growing fish, had smaller heads than those developed at lower temperatures. Mortality was high in the warmest-water groups and may have been selective.

Other differences in shape are known that might seem at first to be the result of environmental irregularities, but more likely have a genetic cause. Some fluvial fishes, particularly cyprinids, display morphological gradients that correspond to degree of adaptation to moving waters (Hubbs, 1941). The forms that inhabit rivers with strong currents are more streamlined; they are terete and have longer, more falcate fins. “Individual populations living in aberrant ecological conditions retain the proper forms, thus showing that these form characteristics are inherited” (Hubbs, 1941). Similar racial differences in morphology, but related to nutritional types, occur in the American poeciliids (especially Mollienisia sphenops); breeding experiments have shown that the differences are hereditary (Hubbs, 1941).

Meristic Variation

The relationship between latitudinal distribution of fish and the number of elements in serially repeated characters gave rise to one of the first and most widely applicable generalizations of ichthyology. Time and again it has been shown that the number of such elements is progressively greater to the north (Hubbs, 1926; Vladykov, 1934; Tåning, 1952; and references therein). Most exceptions have been associated with special local conditions such as colder water currents to the south (Jensen, 1944), differences in altitude in fresh-water systems (Bailey and Gosline, 1955), relatively constant temperature springs (Miller, 1948; Weisel, 1955), differences in time of spawning (Bailey and Gosline, 1955), or salinity gradients (Schmidt, 1917). Sometimes the cline is reversed for one fin only, so that the number of elements in that fin is higher in more southern parts of the distribution.
of the species; the other meristic characters, however, show the expected increase from south to north (Hubbs, 1921, 1926; Schultz, 1927). In the Southern Hemisphere the few cases that have been studied show that the counts increase from north to south, that is, in the opposite direction to that observed in the Northern Hemisphere (Hubbs, 1926; Vladykov, 1934); this increase is related to the reversed temperature gradient. In both the Northern and Southern Hemispheres there is a good correlation between cooler environmental temperatures and higher meristic numbers.

Apparently the number of serial elements is determined by developmental rate (Hubbs, 1926; Gabriel, 1944; and references therein). Longer developmental periods usually produce higher counts in meristic structures. This then is the mode of action of lower temperatures since developmental rate varies directly with temperature. Other agents which retard development, such as high salinities and low oxygen tensions, have effects parallel to those of low temperatures (Hubbs, 1926; Taning, 1952; Seymour, 1956).

Furthermore, those characters which are last to appear during ontogeny are the most labile. The last-formed epidermal plates on the side of the three-spined stickleback, Gasterosteus aculeatus, are the ones lacking in seminude races (Roth, 1920). Caudal vertebrae vary more than abdominal vertebrae (Hubbs, 1922); apparently the caudal vertebrae develop last (Ford, 1933), but this is not certain (Blaxter, 1957). The nape is the last region to be scaled in many fishes, and in certain races of these species it is the commonly naked region (Hubbs, 1926). Fin rays are added, or lost, at the posterior edge of the fin, but not always (Barlow, 1958), and these are the last to appear during development (Hubbs and Hubbs, 1945; Gosline, 1947; Lindsey, 1954).

The number of fin and vertebral elements are determined during a relatively short span of time during early development. Taning (1952) called this the “sensitive” period. Some determination of the counts occurs before this period, but to a much smaller degree. The sensitive period transpires before hatching in salmonid fishes (Taning, 1952; Seymour, 1956), and in Fundulus heteroclitus, the killifish (Gabriel, 1944); however, the sensitive period falls several days after hatching in Macropodus opercularis, the paradise fish (Lindsey, 1954), and in Pleuronectes platessa, the plaice (Molander and Molander-Swedmark, 1957); this may also be the case in Clupea harengus, a herring (Hempel, 1953; Blaxter, 1957), and in Gobius ruthensparri, a goby (Heincke, 1880). The paradise fish has an extremely short incubation period (about two days), and the newly hatched larvae are incompletely developed by comparison with those of the first three groups mentioned above. In the plaice the sensitive period lies near the time of metamorphosis from the pelagic to the benthic stage of the life history. The sensitive period thus appears to be related to some developmental stage, independent of the presence of a protective egg membrane.

The sensitive periods of different structures do not coincide. It is known for Salmo trutta, the sea trout (Taning, 1952), and the plaice (Molander and Molander-Swedmark, 1957) that the vertebrae are determined earlier in development than the fin rays. Also the sensitive periods of the different fins are not the same in the sea trout; this was not investigated in the plaice. In the paradise fish, too, the abdominal vertebrae are fixed considerably earlier in development than are most of the other meristic characters. The number of fin elements is determined at about the same time as the caudal vertebrae (Lindsey, 1954).

Experiments involving only two temperatures, and these not precisely controlled, have demonstrated that the number of countable elements is greater in fish reared at the lower temperature, and
less in those reared at the higher temperature. In these comparisons fish of a relatively uniform genetic background were used. Johnny darters, *Etheostoma nigrum*, reared at the cooler temperature, had more vertebrae than their sibs from the higher temperature (Lagler, in Bailey and Gosline, 1955); each of the temperatures varied over about 2°C. during development. Higher counts of vertebrae and of scales were recorded from *Salmo kamloops* raised at the lower temperature (Mottley, 1934, 1937), but temperatures and oxygen tensions were not well controlled. Dannevig (1950) also found an inverse relationship between two developmental temperatures and the mean number of vertebrae; the temperatures fluctuated considerably. In each investigation the temperatures utilized were reasonably close to the expected temperatures for development under natural conditions.

Two investigators, Gabriel (1944) and Blaxter (1957), observed that vertebral counts of fish reared at several different temperatures were progressively higher in those from the lower temperatures. Gabriel raised killifish, *Fundulus heteroclitus*, at three different temperatures; the mean number of vertebrae was higher at the lower temperatures. Blaxter kept eggs of herring, *Clupea harengus*, at many different temperatures. He counted the myotomes of the herrings at two different developmental stages: at 50% of the embryos hatched, and at 50% with the yolk sac absorbed (myotome numbers were shown to parallel vertebral numbers). Myotome counts plotted versus developmental temperatures yielded a straight line with a negative slope, that is, higher counts at lower temperatures.

Contrary to expectations the number of elements in the dorsal fin of *Lebistes reticulatus*, the guppy, and the dorsal and anal fins of the plaice decrease at lower temperatures. In repeated experiments Schmidt (1919) compared guppies developed at 18°C. with those at 25°C.; fewer dorsal fin rays were formed in fish from 18°C. Observations in nature led Hubbs (1924) to conclude that parallel changes take place in the dorsal fins of two other viviparous cyprinodonts. Molander and Molander-Swedmark (1957) reared two different sets of sibling plaice at 6°C, 8°C, and 10°C. Far fewer elements were formed in the dorsal and anal fins at 6°C than at 8°C. and 10°C. However, the vertebrae responded differently, and this will be considered below.

In some fishes temperature-induced changes do not follow a simple pattern of higher counts at low temperatures, and lower counts at high temperatures. For instance, in salmonid fishes (Schmidt, 1921; Tåning, 1952; Seymour, 1956; and perhaps Mottley, 1937), and in the plaice Molander and Molander-Swedmark, 1957), the mean vertebral number within a genetic stock was in each instance lowest at some intermediate temperature. Progressively higher counts were found at temperatures above and below this intermediate temperature (as in Fig. 1). Thus vertebral numbers plotted as a function of temperature yielded V-shaped curves. The response of the fins to temperature changes in salmonids was similar to that of the vertebrae but more complex. Invariably a V-shaped curve described the relationship between temperatures and counts. In Tåning’s work on the sea trout, however, the V-curves for the dorsal and anal fins were inverted, and strongly asymmetrical. In the dorsal and pectoral fins the inflection of the curve was near the upper end of the temperatures employed, but near the lower end for the anal fin.

Lindsey (1954) found a similar V relationship between temperature and meristic numbers in the paradise fish. Vertebrae, basal elements of the dorsal fin, segmented rays of the anal fin, and pectoral fin rays were all minimal at the intermediate temperature. These counts were higher at the higher temperature as well as at the lower. On the other hand, the
number of anal spines was progressively higher at the lower temperatures. The number of dorsal spines and also of soft dorsal rays was about the same at all temperatures.

Changes in the salt content of the developmental medium can alter the effect of temperature on meristic characters. Heuts (1949a) compared the differences induced by temperature and salinity in fin-ray numbers of the three-spined stickleback, *Gasterosteus aculeatus*. Two genetic stocks were utilized, one a freshwater race, the other a brackish-water race. In one race, the salinity that caused the maximum variation in the median fins with temperature changes coincided with that salinity which produced the minimum variation in the other race, and vice versa. The greater variation in each group occurred at the salinity to which the particular race was best adapted. (It seems probable the restriction of the range of counts in non-adaptive media could have been the result of differential mortality; many fish died before the counts were taken.) Furthermore, when the embryos were reared in the salinities that caused maximum divergence, lower temperatures produced higher median fin counts in each race. At other salinities the relationships were repeatedly altered, and in no predictable fashion. In the pectoral fin the maximum divergences also occurred at the optimal salinities. At all salinities the pectoral fin counts taken from the fish of the fresh-water race were highest in those reared at an intermediate temperature. However, in the brackish-water race the pectoral fin was almost unaffected by changes in temperature at higher salinities.

The hypothesis that meristic characters are dependent on rate of development appears to be valid even in the light of the complex results reviewed in the foregoing. In the poeciliid *Xiphophorus maculatus* the interval between the birth of successive broods averages 31 days, and the modal number of caudal vertebrae is 15; in *X. helleri* the interval is eight days longer, and the mode of the caudal vertebrae is greater by two (Gordon and Benzer, 1945). In four genetically different stocks of chinook salmon, *Oncorhynchus tshawytscha*, the minimum number of vertebrae (but the greatest number of dorsal and anal fin rays) was obtained from fish developed at some intermediate temperature (Seymour, 1956). And the same intermediate temperatures brought about the maximal rate of embryonic growth. Among killifish eggs from a single pair of adults, and at a given temperature, the first fish to hatch had the lowest number of vertebrae (Gabriel, 1944). The fish that developed over a
longer span of time had progressively more vertebrae. In addition, the killifish that developed slowly were larger than those that hatched first. Similarly, in a newly hatched group of siblings of the plaice, *Pleuronectes platessa*, raised at the same temperature, the fish were increasingly larger at each higher vertebral count (Dannevig, 1950). It seems plausible the larger plaice had a longer developmental period than the smaller ones. Among nonsiblings of the plaice, however, no correlation between size and number of vertebrae was evident.

Markmann (1954), using Tåning’s sea-trout material, developed a unique hypothesis to account for variation in vertebral number. It behooves me to criticize his arguments because his hypothesis conflicts with the one presented below. Markmann purported to show that the number of vertebrae laid down by the embryo is directly proportional to the rate of development. The lowest number of vertebrae and the longest incubation period (slowest rate) are said to occur in the fish reared at the intermediate temperature of 6°C. (Fig. 1). The upper curve shows the number of vertebrae and the lower is said to portray the "incubation period"; the latter is plotted reciprocally to convey the notion of rate. But by the "incubation period" Markmann really means the day-degrees of incubation, which is the product of the actual incubation period in days and the particular temperature. The close correspondence between the two curves was assured in the calculations of the "incubation periods" by empirically assuming −0.5°C. as the "biological zero" instead of 0°C. I calculated the true, or absolute, incubation periods from Markmann’s data, and found the rate of development actually increased steadily from the lowest to the highest temperature (Fig. 2). Furthermore, the $Q_{10}$ decreases at each temperature, which means that the incubation period at 6°C. really shows the greatest decrease (increase of rate) relative to the developmental rate at 3°C.

Then I formed a new day-degree product using the Kelvin temperature scale instead of the Celsius scale. This has the advantage of avoiding the arithmetical difficulties that arise as the numbers approach zero. This time the relationship between actual incubation period and temperature was preserved (Fig. 2). Undoubtedly the apex obtained by Markmann is an arithmetical artifact. There is no point in further criticism except to note that Markmann's hypothesis rests primarily on the presumption, derived from this artifact, that metabolism is lowest at the intermediate temperature of 6°C. This is also unlikely on purely physiological grounds because 6°C. is near the thermal optimum for development in this species. Markmann showed, for instance, that the sea trout reared at 6°C. achieved the greatest weight.

Heuts (1949a) has criticized the original hypothesis of Hubbs that developmental rates determine the number of meristic elements. The results he obtained with...
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sticklebacks raised at different temperatures seemed to him to be incompatible with this hypothesis. The first criticism was that the lengths of the embryonic lives of two genetically different races of sticklebacks were the same, although meristic characters were different. However, Heuts has not determined the sensitive period (Tânิง, 1952) for the characters involved. This period need not occur before hatching (Lindsey, 1954). Without considering this, he transferred the fish of both races to fresh water right after hatching for further development. If, as he proved for the eggs, fresh water imposes a selective stress on the different races, then modification of the meristic characters conceivably still could be operating after the transfer. Further, mortality was appreciable before and after hatching and certainly could have been selective. As Heuts (1947) has pointed out, there is a strong correlation between morphological characters and degree of adaptation to different salinities in these fishes. And beyond these arguments the races are genetically different; the relationship between growth rate and differentiation of parts could be inherently dissimilar and hence produce different counts even though the two groups have equally long embryonic periods. Hubbs's contention that developmental rate determines the number of elements formed was clearly intended for those cases where a given genetic system is under consideration.

The second criticism put forth by Heuts (1949a) was that changes in salinity at a given temperature did not influence the developmental rates, but did modify the number of elements produced. It can be seen (Heuts, 1947a) that the percentage of eggs that survive to hatching is clearly different, depending on the salt content of the developmental medium. Once more, differential mortality is a serious objection. And so is the immediate transfer of the fish to fresh water upon hatching. In all fairness to the splendid work done by Heuts, the problem of differential, probably selective, mortality is the greatest difficulty to overcome in this type of experiment. Certainly differential mortality has not been obviated in most investigations of this problem. Only Tânǐng has had success in this respect.

Developmental rates are thought by Hubbs (1926) and Gabriel (1944) to determine meristic characters through the control of two different aspects of developmental physiology, to wit, growth and differentiation. In this scheme low temperatures retard growth more than differentiation. When the growth is slowed, the presumptive tissues presumably develop into a greater number of elements before the segments are fixed; conversely, rapid growth does not permit the differentiation of as many elements.

A model for the interaction between growth and differentiation can be envisioned along slightly different lines. Conceivably each structure has, in differing degrees, its own particular sensitivity. The differentiation of these structures may be more or less interrelated, as indicated by parallel changes in the median fins and vertebrae in some fishes. When the number of elements increases at lower temperatures, the differentiation of the structure is assumed to be less sensitive to the environment, not more, than is overall growth. As an example, let the differentiation of the vertebrae have a low temperature coefficient ($Q_{10}$ or $\mu$) and the growth of the embryo a high coefficient. Then growth will be retarded by low temperatures, but the rate of formation of vertebrae will be less diminished. Hence the vertebrae will form over a relatively longer period of time and more of them will be laid down. On the other hand, those characters which decrease in numbers at low temperatures, such as the dorsal fin rays in the guppy, could be explained on the basis of their having higher sensitivities (higher $Q_{10}$) to the environment than has total development.

This model would allow for the
V-shaped curves obtained by Tåning (1952) where the apex of the V falls at different temperatures for different fins and the vertebrae. These curves would be interpreted as showing points of inflection of the temperature coefficients. Seen in this manner the curves are reminiscent of the complex interactions between activity optima of different enzymes within a given system. This argument could be developed in like fashion to take into account the effects of other growth retarding factors such as high salinity, low oxygen tension, and the amount and duration of light exposure.

This model has wide application in that it is compatible with observed reverse and V-shaped relationships; otherwise, it is clearly identifiable with the original argument advanced by Hubbs (1926). It should be made clear, too, that this is not an explanation of how the differences are actually brought about; it is only a model. It is also consistent with the results of experiments involving “temperature shocks” (Tåning, 1952), especially if thermal acclimation is taken into consideration.

If fish are transferred from one temperature to another just before the sensitive period, the meristic characters are greatly modified, far more so than if the fish had been reared continuously at the second temperature (Tåning, 1952; Lindsey, 1954; Molander and Molander-Swedmark, 1957). The most significant feature of these manipulations is that the direction of induced changes in counts is extremely consistent. The number of elements always is increased when the transfer is from a higher to a lower temperature, and consistently fewer elements form when the fish are transferred from the lower to the higher temperature. It is worth noting that it was exactly these workers who discovered the complex temperature/fin-count relationships in fishes reared at constant temperatures.

Apparently the embryo is acclimated (Bullock, 1955, has reviewed acclimation phenomena) to the first developmental temperature. Sudden transfer to water having a different temperature, higher or lower, must result in a metabolic response in excess of the normal or acclimated level. Subjected to the same thermal shock, the differentiation of the meristic characters evidently has a lower sensitivity. Consequently transfers to higher temperatures produce lower counts, to lower temperatures, higher counts. In every instance (Tåning, 1952; Lindsey 1954; Molander and Molander-Swedmark, 1957) the results agree with this explanation.

Under uniform developmental temperatures the relationship between the temperature coefficients of growth and of differentiation are variable (as in the complex responses in trout, stickleback, and paradise fish). On the other hand, when temperature changes occur during development the temperature coefficient of growth processes appears to be higher (more labile) than that of differentiation. Thus when temperatures oscillate, particularly if too fast to allow for acclimation, the expectation is that a decrease in temperature will increase meristic characters; an increase will decrease the counts. This may resolve some of the conflicts between observations taken in nature and those in laboratories. The experiments of Heuts (1949a), Tåning (1952), and Lindsey (1954) for example, showed that the relationship between temperature and different meristic characters is complex when the temperatures are rigidly constant. Yet observations on the stickleback and sea trout from nature revealed a gradient of decreasing counts from north to south, hence from cool to warm temperatures. It should almost go without saying that constant temperatures are not natural.

Lindsey (1958) has suggested the north-south clines may be induced by changes in the amount of light impinging on the eggs because this environmental parameter varies more regularly with latitude.
than does water temperature. Increased intensity (McHugh, 1954) and increased duration (Lindsey, 1958) of light caused the development of a lower number of vertebrae in two unrelated species of fishes. However, in these experiments many of the embryos died and selective mortality again may have been involved. A further reservation lies in the nature of the material. Both species used in these experiments, the grunion, *Leuresthes tenuis*, and the kokanee, *Oncorhynchus nerka*, deposit their eggs below the surface of the substrate. As a result the eggs normally develop in total darkness. The metabolism of these embryos might be unusually susceptible to the effects of increased illumination. In the experiments by McHugh, the physiology of the developing fish may have been adversely affected by the total elimination of clues to daily (circadian) periodicity. Constant light and temperature conditions are known to be inimical to the physiology of certain organisms (Pittendrigh, pers. comm.). It is worth noting, too, that some clines run in directions other than north-south. Bailey and Gosline (1955) found for many percid fishes that the best trends for shifts in vertebral numbers ran southwest-northeast. Until more experiments are available the role of light in producing clines will have to remain an open question.

Up to this point the discussion has centered on variability induced in meristic characters of the phenotype, without regard to the genotype. A genetic determination of meristic characters has been demonstrated both within and between populations, or races. According to Hubbs (1955) the dorsal and anal fin ray numbers in the subspecies of the mosquito fish, *Gambusia affinis*, are determined by the action of a single gene; the validity of this assertion has been questioned by Gordon (1957). In all other instances the characters behave as though determined by a multifactor system; undoubtedly, this is the usual situation. The progeny of the killifish, *Fundulus heteroclitus*, with high vertebral numbers also have high counts, and likewise for those from killifish with low counts (Gabriel, 1944). In the same way, the number of dorsal fin rays of new-born guppies is high or low depending on the parentage (Schmidt, 1919; Svärds, 1945). Hybrids between races of the same species commonly have intermediate numbers of elements (Heuts, 1949a; Svärds, 1953; Hubbs, 1955). Successive generations of a race of *Zoarces viviparus* transferred to a new environment continued to be recognizable from the endemic population on the basis of different vertebral and median fin counts (Ege, 1942). Different races of species reared under comparable conditions have dissimilar meristic characters (Mottley, 1937; Heuts, 1947b, 1949a; Seymour, 1956).

There have been numerous studies on natural populations of fishes. Sometimes it has been shown through investigation of meristic characters that genetic differences exist between the populations in question. Since the literature is large and the results variable I will restrict my comments to my own research (Barlow, 1958). Within a given year-class of a gobiid fish, *Gillichthys mirabilis*, there is no correlation between the pectoral and median fin counts. However, in successive year-classes shifts in the means of pectoral fins are paralleled by shifts in the means of the median fins. Fish developed in cold years show increases in the average pectoral fin count as well as in the means of the median fin counts. Thus the number of elements in each set of fins is independently determined. However, from population to population the number of elements in the pectoral and median fins is significantly negatively correlated, and in a regular way. The pectoral fin cline runs in the opposite direction to that of the median fins. Furthermore, *mirabilis* transferred from San Diego to the Salton Sea, a saline desert lake on almost the same lati-
tude, showed a tremendous increase in the counts taken from all fins. Remarkably, the ratio of pectoral fin rays to median fin rays remained the same, showing that the mean relationship between fins was unaltered. Thus the meristic cline apparently corresponds to a genetic cline. Studies on the metabolic physiology of different populations support this contention.

The variance of a given fin, or of the vertebrae, may be a parameter of greater utility than the mean. Within a given population of *Gillichthys mirabilis* the change in means may show significant differences from year to year. The variance, however, remains the same. Also, northern populations of *mirabilis* manifest greater fin-ray-count variation than do the southern populations.

Then if genetic differences underlie the meristic dissimilarities which exist between populations, or races, a question immediately comes to mind: are these changes in fin ray counts adaptive? We can disregard for the moment the problem of whether it is the observed difference itself that has selective value.

The transplantation experiments of Ege (1942) constitute perhaps the best demonstration of selection for fish with a particular number of vertebrae. One race of *Zoarces viviparus*, with a low vertebral count, was introduced into the enclosed habitat of another race, with a high count. So many fish of the first race were introduced that they were the dominant form. The first few year-classes showed a rise in the mean number of vertebrae. Then the mean decreased in succeeding years. A pronounced reduction in the number of vertebrae took place between birth and the age of one year in each of the year-classes. The mean value per year-class decreased from one-half to one and one-quarter vertebrae. Ege realized this meant a change in the genotype between the young and the adults of the same year-class. The selection was for fish with the lower vertebral number.

Laboratory reared stocks of a given fish species show greater variability than do the naturally occurring populations. Fin counts of laboratory reared cottids, *Clinocottus recalvus*, have a much greater range than do their natural counterparts (Morris and Scheer, 1957). Gabriel (1944) noted that even though he could experimentally produce high or low vertebral numbers in *Fundulus heteroclitus*, the count in the wild population was usually less variable than that in the laboratory. The vertebral mode of the wild population of *F. heteroclitus* was 32; the range was four. In the experimental fish the range was as low as four in one experiment but ran up to six and eight in the others. This is more striking with the realization that, in contrast to the fish from nature, each laboratory sample consisted of siblings reared at a uniform temperature and salinity. This implies the extremes had been present in the natural population but were eliminated, as would be predicted if the populations were genetically homeo-static (Lerner, 1954). From studies of specimens collected from nature Bailey and Gosline (1955) concluded that natural selection reduces the variability of vertebral numbers in a percid fish.

It is difficult to believe that the addition or subtraction of a few elements would materially affect the probability of the survival of a fish, though this may be the case. However, it is difficult to prove, or disprove, such a thesis.

The more profitable, but indirect, attack on this problem is to determine whether or not there is a correlation between meristic characters and obviously adaptive physiological processes. In the carp, *Cyprinus* (sp.?), certain genotypes that are said to be more viable than others were recognized by the degree and pattern of squamation (Kirpichnikov, 1945). Golovinskaya (1940) reported a mutant gene in the carp that appears to have the pleiotropic effect of reducing vitality while decreasing the number of fin rays, scales, and gill rakers.
In four different races of the chinook salmon, *Oncorhynchus tshawytscha*, the vertebral counts were clearly different when the fish were reared under the same conditions (Seymour, 1956). The divergence in vertebral counts due to genetic dissimilarities between the races was greater than that induced within the phenotypes. In each race the optimum temperature for development (fastest development, lowest mortality, fewest aberrant fish) was different. Thus in *Oncorhynchus* genetic differences connected with the determination of vertebral numbers were correlated with adaptive changes in thermal responses.

In the stickleback, *Gasterosteus aculeatus*, physiological characteristics are correlated with lateral shield numbers as well as with vertebral numbers (Heuts, 1947a). Adults of the race adapted to fresh water are smaller and have far fewer lateral shields and slightly more vertebrae than the adults of the brackish-water race (Heuts, 1947b). The physiological characteristic studied was successful embryonic development in waters maintained at various constant salinities and temperatures. The embryos of the brackish-water race were generally better adapted for development at higher salinities than were the embryos of the freshwater race. The complex nature of the results, though, leaves the matter an open question. However, later experiments (Heuts, 1956) with a geographically different race yielded a similar type of variation and consequently increase the confidence in the earlier experiments. The fresh-water and brackish-water races are interfertile and cross matings are thought to take place in nature, though at a low frequency. Hybrids between the races are morphologically intermediate, but physiologically they are the same as the maternal race.

Hubbs (1928) recognized the possibly genetic nature of clines of meristic characters in fish species. He advanced the hypothesis that differences in counts between geographically separated populations are indications of adaptive changes. In an extension of the ideas of Baldwin (1896), Hubbs suggested that species new to an area would be altered by the environment, and that these differences, being associated with adaptive changes, would become genetically fixed. The evidence for genetic differences between races, and for the adaptive significance of such changes, has been cited above. I would not care to extend the argument that meristic clines are genetically determined to include all the meristic clines that have been described for sundry fishes. However, I think it highly probable that genetically reinforced differences exist in those species where the populations are somewhat isolated from one another. This would include fresh-water forms, species from marine bays, and the shore species of oceanic islands. Pelagic marine species on the other hand probably are as panmictic as could be expected within each oceanic system or subsystem.

**Summary**

Variation in shape of fishes is poorly understood, but in general retarded growth seems to cause small heads and associated parts, and short fins.

In the meristic characters, slow development is commonly associated with high numbers of elements, fast development with low numbers. Different factors in the environment, such as temperature, salinity, and oxygen, may control the rate of development. The number of elements is determined during a short “sensitive” period in the embryonic, or larval, fish.

Plots of temperature during development versus number of elements formed, in precisely conducted experiments, have revealed a family of V-, or inverted V-shaped curves. However, changing the temperature just before the sensitive period always produced an increase in the counts when the temperature was lowered, and a decrease when the temperature was raised. The rate of differentia-
tion of each meristic character is thought to be more or less independent of the other meristic characters in its relationship to the overall growth of the embryo. Inflection points on the curves indicate reversals in the relationships. Disagreements in findings from the field and from the laboratory may be the result of monotonous, uniform conditions in the laboratory, an unnatural and possibly harmful situation. Experiments are needed which employ controlled, fluctuating parameters of the environment.

Genetic determination of variation in meristic characters has been demonstrated through typical breeding experiments, hybridization, and transplantation. It has also been deduced by comparing the nature of variation within a given year-class, between successive year-classes, and between populations.

The variation itself may be a more stable and useful indicator of genetic determinants than the mean.

Regular changes in counts, such as in geographical clines, probably reflect adaptive changes of a genetic nature.

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